# Long-term change in the distribution of Japanese sardine in the Sea of Japan during population fluctuations

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ABSTRACT: The distribution of small pelagic fish species changes in association with fluctuating stock biomass. We analyzed the spatio-temporal dynamics of Japanese sardine Sardinops melanostictus inhabiting the Sea of Japan during periods of stock biomass fluctuation using generalized additive models (GAMs). Logbook data from drift gill net surveys and large- and medium-type purse seine fisheries, conducted from 1970 to 1999, were used. A 2-step data analysis was performed: (1) for the presence or absence of sardine, and (2) for the catch per unit effort (CPUE) where fish were present. The explanatory variables in the GAMs were year, longitude/ latitude, sea surface temperature, and fishing method. The best model based on Akaike's information criterion showed that the likelihood of high sardine presence was limited to areas around the Oki and Tsushima Islands in the early 1970s. However, these areas expanded south along the coast and offshore to the north until the mid-1980s. Subsequently, sardine presence contracted to the initial distribution areas during the mid-1990s. Over the 30 yr period, the spatial distribution of the CPUE changed minimally for both fishing methods. Compared with the trajectory of stock biomass, the potential distribution area began expanding during the initial phase of population expansion, and started contracting before biomass peaked. There was a time lag between the peaks of distribution area and biomass. In conclusion, we discuss how changes to oceanographic conditions in response to a climate regime shift may influence the distribution of Japanese sardine in the Sea of Japan.

KEY WORDS: Japanese sardine  $\cdot$  Sardinops melanostictus  $\cdot$  Spatio-temporal dynamics  $\cdot$  Generalized additive model

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# **INTRODUCTION**

Small pelagic fish species, which are short-lived and fast-growing, have been characterized by marked fluctuations in stock size, such as multidecadal productivity cycles (Schwartzlose et al. 1999, Jacobson et al. 2001, Barange et al. 2009). Fluctuating stock size has been associated with environmental changes in oceanic conditions from basin to global scales (Lluch-Belda et al. 1989). Spatio-temporal dynamics and the life-history traits of fish populations have been studied in relation to fluctuating stock size. For example, the packing density and area occupied by sardine and anchovy populations off the coasts of California (USA), Peru, South Africa, and Japan (northwest Pacific Ocean) increased with population growth (Barange et al. 2009). The distribution of pelagic fish is governed by habitat selection and migration, which change with environmental factors (Fréon & Misund 1999). Thus, understanding the factors that determine fish distribution, and how distribution is related to stock biomass, could help explain fluctuation in catch rates and the extent to which fisheries are exploiting fish stocks. Such information could help improve the precision of stock assessments and the management of commercial fish stocks (Fréon & Misund 1999).

In Japan, catches of Japanese sardine *Sardinops melanostictus* have been documented for almost 450 yr (Ito 1961). Japanese sardines are divided into 2 large subpopulations according to their distribution: one subpopulation inhabits the Sea of Japan and the East China Sea, whereas the other inhabits the northwest Pacific Ocean (Kuroda 1991). The 2 subpopulations have different biological and ecological characteristics (Wada & Jacobson 1998, Ohshimo et al. 2009), even though no genetic differences have been found (Okazaki et al. 1996). For both subpopulations, catch rates increased from the 1970s and peaked in the late 1980s, but then noticeably declined during the early 1990s (Wada & Jacobson 1998, Ohshimo et al. 2009).

When stock biomass increased, the spawning grounds of the northwest Pacific subpopulation expanded offshore (Kuroda 1988, Kawai 1994, Barange et al. 2009). Thus, the distribution area of the fish subpopulation expanded in relation to changes in stock biomass, assuming that the presence of eggs and larvae collected from these areas was linked to the distribution of adult fish (Barange et al. 2009). Furthermore, the fishing ground of the purse seine fisheries in the northwest Pacific became more widely distributed when stock biomass was high (Wada & Jacobson 1998), reflecting the expansion in the distribution of the sardine population.

In contrast, knowledge of changes in the spatiotemporal distribution and the life history traits of the Sea of Japan subpopulation remains limited. Sardine catch data, using drift gill net monitoring surveys from the 1980s, are available for the northern and offshore areas of the Sea of Japan (Hiyama 1998). This dataset may provide important information on changes in the distribution when stock levels were high. However, the area of the survey did not cover the whole distribution area of the sardine subpopulation, particularly the southern coastal area. In addition, quantitative analysis of annual changes in the distribution area has not been conducted (Hiyama 1998).

Other data were also spatially limited and were not detailed enough to evaluate changes in the distribution of the Sea of Japan subpopulation. For instance, the Japanese large- and medium-type purse seine fishery provides long-term catch records of Japanese sardine in the southern Sea of Japan and the East China Sea. In general, commercial catches may not always be proportional to stock abundance, because they reflect fishermen's behavior in addition to stock abundance (Harley et al. 2001). Catch per unit effort (CPUE) presents the distribution of catch but sometimes needs to be standardized with respect to fishing characteristics, since it comprises the spatial distribution of fish and the allocation of fishing effort. However, presence or absence of Japanese sardine in the catch record could be considered as a proxy for potential distribution, since the purse seine fishery targets various pelagic species over a broad area.

To compensate for the spatial biases of these data and to capture the spatio-temporal dynamics of Japanese sardine in the inland seas, the integration of data from the 2 sources is useful. The entire distribution of sardine can be evaluated by integrating the presence/absence data from both drift gill net surveys conducted in the northern and offshore area in the Sea of Japan and purse seine fisheries in the southern and coastal areas in the Sea of Japan. Spatio-temporal generalized additive models (GAMs; Hastie & Tibshirani 1990) have recently been used to map the distribution of fish and to investigate relationships between environmental factors and distribution patterns (Palialexis et al. 2011, Bartolino et al. 2012, Mourato et al. 2014, Ohshimo et al. 2017).

In this study, we examined the spatio-temporal dynamics of Japanese sardine inhabiting the Sea of Japan from the 1970s to the 1990s, when stock biomass fluctuated, using a 2-step analysis of the sardine catch data. First, we developed GAMs to evaluate long-term changes in potential distribution using the presence/absence of sardine in catch records from gill net surveys and purse seine fisheries. Second, we developed GAMs to evaluate the spatiotemporal changes in non-zero catch distribution using CPUE for each fishing method. We also examined the dependence of fish dynamics on sea surface temperature (SST) by incorporating it in the models and discuss the possible influences of other environmental factors.

# MATERIALS AND METHODS

## **Biological and environmental data**

We analyzed catch records from drift gill net monitoring surveys and large- and medium-type purse seine fisheries from 1970 to 1999, when sardine stock biomass highly fluctuated (Table 1). The data from March to May were used, which coincided with sarSea of Japan from March to May, 1970 to 1999. CPUE: catch per unit effort

Table 1. Summar	y of the dataset use	d in the generalized	additive model ana	lyses on the distribut	tion of Japanese sar	dine in the

Data source	Purse seine Commercial fishing	Gill net Scientific survey
Number of operations	91063	3162
Number of locations	4257	3162
Number of locations with sardine presence	2670	1140
Data unit used in the analyses	Location	Operation
Period of the analysis for presence/absence	1970-1999	1970-1999
Period of the analysis for CPUE	1970-1999	1975-1992
Annual mean ± SD number of data units in the analysis for presence/absence	$141.9 \pm 23.3$	$105.4 \pm 56.4$
Annual mean ± SD number of data units in the analysis for CPUE	$89.0 \pm 36.9$	$63.3 \pm 35.3$

dine northward migration (Ito 1961). Scientific gill net surveys were conducted from March to May between 1964 and 1999 in the northern, and relatively offshore portion of the Sea of Japan, mainly to estimate salmon distribution (Fig. 1). The number of salmon and sardine caught, the number of net panels, SST, and the latitude and longitude were recorded for each survey (Table 1). The mesh size of the gill nets was generally between 91 and 100 mm. Japanese sardine are usually caught in gill nets that have a mesh size larger than or equal to 55 mm (Sato et al. 2015).



Fig. 1. Research and fishing locations in the Sea of Japan. Crosses indicate the stations where gill net surveys were conducted. Open circles indicate the fishing locations of large- and medium-type purse seine fisheries. The 2 polygons indicate the area where operations were conducted repeatedly across the study years. Surface current systems of the Tsushima Warm Current (after Senjyu 1999) and the polar front in May (after Japan Meteorological Agency www. data.jma.go.jp/gmd/kaiyou/data/db/maizuru/knowledge/ tsushima\_current.html) are illustrated

The large- and medium-type purse seine fishery targets small pelagic fish (mainly horse mackerels, mackerels, and sardines) throughout the year. The fishing ground is widely distributed in the coastal area of the Sea of Japan and the East China Sea. The current analysis used the data that fell between the latitude and longitude ranges of 30-45° N and 128-141°E, to focus on sardines inhabiting the Sea of Japan and adjacent waters (Fig. 1). Fishers distinguished the catch of small pelagic fish into 7 species and recorded their weight. The weights of catches and the number of operations were summed for each month at each location (latitude and longitude) at a resolution of 0.5°. Logbooks were available for the East China Sea and the southern part of the Sea of Japan since 1967 and for the northern Sea of Japan since 1978. SST was derived from temperature data that corresponded to the same year and month from an adjacent location at a resolution of 1° in latitude and longitude, published by the Japan Meteorological Agency (www.jma.go.jp/jma/indexe.html). Purse seine fisheries generally use an echo sounder and fishing light to find and collect fish, methods which may produce biases. However, we did not consider those factors in the present analysis due to the lack of detailed information on fishing methods. Nevertheless, the catch record provides useful information on quantitative spatio-temporal dynamics, since the purse seine fishery is the only information source for sardines that has been collected over a broad area for a long time.

# **Two-step analyses**

Owing to the high percentage of zeros in the catch data (64% for the gill net surveys and 54% for the purse seine fisheries), we could not obtain reliable results, even when zero-inflated models were adopted for the combined data from the 2 fishing methods. Therefore, we performed a 2-step analysis of the sardine catch data.

The first level examined binomial data, accounting for the presence and absence of sardines in the catch records. At this level, the model could take into account both gill net surveys and purse seine fisheries, and thus cover a wider area. The area with sardine presence was considered an index of potential distribution area. The locations where sardine catches were recorded, irrespective of number and weight, were scored as sardine presence. Alternatively, the data with no records of sardine catch were considered to indicate sardine absence.

The second level of our analysis examined the density of non-zero catches by each fishing method. CPUE was used as a density index, by calculating the number of sardines caught per number of net panels used per each operation for gill net surveys or the monthly weight of sardine caught per number of fishing operations at each location for purse seine fisheries. The gill net survey data from 1970 to 1974 and from 1993 to 1999 were omitted from the second level analysis because of zero or very few sardine catches (Table 1). Data were also removed from the analysis when the number of nets was not recorded or when the gill net was hauled within a few hours because of rough sea conditions (the standard soak time of a gill net for a given survey was 12 h).

## Generalized additive models

For the presence/absence data, the effect of year, location, SST, and fishing method was examined by a GAM with a binomial error distribution that had a logit-link function. A full model for presence probability  $(0 \le y \le 1)$  was:

$$\log\left(\frac{y}{1-y}\right) = s(\text{year})_{\text{ID}} + s(\text{lon,lat}) + s(\text{lon,lat})_{\text{year}} + (1)$$
$$s(\text{SST}) + s(\text{SST})_{\text{year}} + \text{ID}$$

and consisted of the spline smoother of year for each fishing method (ID). The spline for longitude/latitude represented the common component of the effect of spatial location through study years as an isotropic bivariate function (Wood & Augustin 2002). In addition, the interaction of spatial location and year was evaluated by the splines of longitude/latitude for each year, and the interaction of SST dependence and year was evaluated by the splines of SST for each year. The effect of fishing method (ID) was also incorporated as a category variable. For the CPUE data per fishing method, the effect of year, location, and SST was examined by a GAM with a gamma error distribution with a log-link function. The full model had the spline smoothers for year, longitude/latitude, SST, and interaction of longitude/latitude and year and that of SST and year.

Stepwise selection was performed to determine whether a variable should be removed from the GAM based on Akaike's information criterion (AIC). A model was also removed from a candidate model set if the parameter estimation failed to converge.

# Model evaluations

The performance of the presence/absence model was evaluated by receiver operating characteristic (ROC) curve analysis. The ROC curve plots the sensitivity (the correctly predicted positive fraction) to the 1 – specificity (the correctly predicted negative fraction) of a diagnostic test (Hanley & McNeil 1982). The different points on the curve correspond to the different thresholds used to determine whether the test results are positive. The area under the ROC curve (AUC) summarizes the overall diagnostic accuracy of the test and indicates excellent discrimination if it is close to 1 (Hosmer & Lemeshow 2000).

The AUC of the full model, in which all available data were used in both training and testing, was calculated. In addition, the mean and standard deviation (SD) of the AUC were calculated for 100 crossvalidation models, in which 100 randomly generated partitions of 70% training and 30% test data were used. The partitioning technique was based on the holdout partition, where selection was weighted to reflect the true proportion of presence/absence (Kohavi 1995, Manel et al. 1999).

The AUC is widely used as a statistical metric for model performance, but is sometimes criticized because it is assessed over all thresholds, some of which may not be relevant (Lobo et al. 2008). To avoid a bias in performance assessment, we also calculated 3 threshold-dependent indices at a given threshold for the best model: sensitivity, specificity, and percent correctly classified (PCC) (Fielding & Bell 1997, Manel et al. 1999, Howell et al. 2016). We determined the optimal threshold as the value at which the average of the 3 performance indices reached a maximum according to 5 thresholding methods: sensitivityspecificity equality, sensitivity-specificity sum maximization (MSS), ROC-plot based approaches, prevalence, and average probability/suitability approaches (Liu et al. 2005, Howell et al. 2016).

The performance of the CPUE model was evaluated by the fit of the predicted values to the observed values. Finally, we assessed the degrees of contribution of each explanatory variable using delta AIC ( $\Delta$ AIC) for the presence/absence and CPUE models.

# **Model predictions**

The spatio-temporal changes in sardine presence and catch density were assessed based on the output of the best model. For model predictions, 2 polygons were defined to cover the stations where either the purse seine fisheries or the gill net surveys were conducted intensively across years, to avoid extrapolation of the model (Fig. 1). The grid points inside each polygon were set at intervals of 0.5° in longitude and latitude.

The annual presence probability was predicted for each fishing method at each grid point within each polygon, using the best model for presence/absence data. SST was assumed as the average observed SST values from March to May in a given year. If the grid point belonged to both polygons, presence probability was determined from the average of 2 probabilities predicted for each of the 2 fishing methods.

The annual CPUE for each fishing method was predicted for each grid point within each polygon by the best model for CPUE data, assuming average SST from March to May in a given year.

The area of sardine presence is likely to reflect its potential distribution area. We calculated the fraction of the grid points with sardine presence, defined as presence probability over an optimal threshold (determined by model evaluation), to all points belonging to the 2 polygons. To compare temporal changes in the distribution area and stock biomass, we used the estimated biomass of Japanese sardines in the Sea of Japan and East China Sea using a cohort analysis (Ohshimo et al. 2009).

All of the analyses were carried out in the statistical software R version 3.3.0 (R Core Team 2016) with the 'mgcv' library (Wood 2006), 'PresenceAbsence' library (Freeman & Moisen 2008) and 'mldr' library (Charte & Charte 2015).

## RESULTS

### Presence or absence of sardines

The best model of sardine presence included a function of year depending on the fishing method,

longitude/latitude, SST, the interaction of spatial location and year, and the interaction of SST dependence and year (deviance explained = 54.1%, variables in Table 2, and see Tables S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m593p141\_supp. pdf). Thus, the probability of encountering fish changed both spatially and temporally, with SST dependence also changing temporally. The interaction of longitude/latitude and year and the effect of year demonstrated high  $\Delta$ AIC values (Table 2).

The partial response curve of year was relatively constant over a long time period for the purse seine fisheries (Fig. 2a), but exhibited an abrupt change for the gill net surveys, with a rapid increase for a few years after 1975, followed by a sharp decrease after 1983 (Fig. 2b).

The annual partial response curve of SST showed a positive effect for sardine presence at a wide range of SSTs when the observed SST range was considered (0.5°C to 23.8°C; Fig. 3a illustrates an example from 1984, showing a typical curve shape). The partial response curves of SST had the same shape for the 2 fishing methods, with the purse seine fishery being used as an example in Fig. 3. SST at the lower limit of the positive effect fluctuated from 4.7 to 13.7°C, but SST at the upper limit was greater than 13.2°C and mostly exceeded 23.8°C (Fig. 3b).

#### Model evaluation: presence/absence

The AUC score for the best model (0.934) was excellent (range 0.9–1) and the mean of the cross-validation AUC score (0.883) was good (0.9–0.8; Hosmer & Lemeshow 2000), with low SD (0.008). The optimal threshold was 0.46, given by MSS. The best model

Table 2. Approximate significance and change in Akaike's information criterion ( $\Delta$ AIC) of each explanatory variable of the best model for the presence and absence of sardines (deviance explained = 54.1%). ID indicates the fishing method: 1 is purse seine fishery and 2 is gill net survey. Lon, lat: longitude, latitude; SST: sea surface temperature. Summary of the smooth terms for (lon, lat)<sub>year</sub> and SST<sub>year</sub> is provided in Table S1 in the Supplement. The top 5 models for the presence and absence of sardines are provided in Table S2

Smooth terms	edf	Ref.df	$\chi^2$	р	ΔΑΙϹ
year <sub>ID=1</sub> year <sub>ID=2</sub> (lon, lat) (lon, lat) <sub>year</sub> SST SST <sub>year</sub>	9.00 8.19 20.88 8.89	9.00 8.61 24.35 8.99	106.98 195.50 159.17 139.50	<0.001 <0.001 <0.001 <0.001	337 85 427 39 118



Fig. 2. Partial response curves showing the effect of year on the probability of sardine presence for (a) large- and medium-type purse seine fisheries, and (b) gill net surveys. The *y*-axis represents the standardized partial regression coefficient. Dashed curves indicate 95% confidence intervals

showed good performances (>0.8) for sensitivity (0.917) and PCC (0.854), and fair performance (0.7-0.8) for specificity (0.786) at the optimal threshold.

## Model predictions: presence/absence

The observed presence probabilities of Japanese sardine changed on a decadal scale in the Sea of Japan (Fig. S1). Therefore, the predicted presence probabilities are illustrated by mean and SD maps, per decade per grid point at 0.5° longitude and latitude intervals in Fig. 4.

Fig. 3. (a) Partial response curves showing how sea surface temperature (SST) in 1984 affected the probability of sardine presence for large- and medium-type purse seine fisheries. The *y*-axis represents the standardized partial regression coefficient. Dashed curves indicate 95 % confidence intervals. (b) Annual changes in the effect of SST on large- and mediumtype purse seine fisheries. Dashed line with filled circles indicates the range of SST with positive standardized partial regression coefficient

1995

2000

In the 1970s, the mean presence probability was over 0.46 in the areas around the Oki and the Tsushima Islands (Fig. 4a-1), but not in the northern region (Fig. 4c-1). However, the SD of presence probability was greater along the coasts of Kyushu and Honshu Islands and in the middle part of the Sea of Japan (Fig. 4b-1,d-1). This indicated that sardines started to be present there in the late 1970s, when the presence probability of sardine became higher (see also Fig. 2).

In the 1980s, the area with a high probability of catch ( $\geq 0.8$ ) expanded southwards along the coasts, covering a broad area in the southern Sea of Japan, with small SD values (Fig. 4a-2,b-2). In addition, the northern boundary of sardine presence moved northwards and offshore (Fig. 4c-2), but was south of the polar front, which was located between the Tsushima Warm Current (TWC) and the Liman Cold Current at approximately  $38-40^{\circ}$  N (Fig. 1). Large SD values in

the northern Sea of Japan illustrate that sardine presence expanded northwards and offshore in the first half of the 1980s, but contracted southwards and towards shore in the late of the 1980s (Fig. 4d-2 and also see Fig. 2b).

In the 1990s, the probability of sardine presence remained relatively high around the Oki and the Tsushima Islands, with relatively large SD in the offshore region (Fig. 4a-3,b-3). In comparison, sardines were absent from the northern offshore region (Fig. 4c-3), but the large SD in the middle of the Sea of Japan in-



Fig. 4. (a,c) Mean and (b,d) standard deviation maps of predicted presence probability per decade per grid point at a 0.5° longitude and latitude interval. (a) and (b) are for large- and medium-type purse seine fisheries, (c) and (d) are for gill net surveys. The color bar indicates the probability

dicated that sardines remained in these regions in the early 1990s (Fig. 4d-3 and also see Fig. 2b).

Thus, the areas around the Oki and the Tsushima Islands were considered the central distribution area for Japanese sardine inhabiting the Sea of Japan and adjacent waters.

## Sardine CPUE

The best models of CPUE included a function of year, longitude/latitude, SST, and the interactions of spatial location/SST dependence and year for both purse seine fisheries (deviance explained = 69.5%; Table 3, and see Tables S3 & S4 in the Supplement) and gill net surveys (deviance explained = 52.3%; Table 4; Tables S5 & S6).

The partial response curve of year for the purse seine fisheries was positive after 1981, and peaked around 1990 (Fig. 5a). The gill net surveys showed an abrupt increase after 1980, a peak during the early 1980s, and then a decline during the late 1980s (Fig. 5b). There was a time lag between the peaks of the 2 trajectories.

The interaction of SST dependence and year contributed the second highest degree for purse seine fisheries (Table 3). However, the annual partial response curve generally showed a monotonous decrease with SST (an example in 1987 is illustrated in Fig. 6a because it shows a typical curve shape) and was almost positive within the observed range ( $6.4-23.7^{\circ}$ C) after 1976 (Fig. 6b). In comparison, the interaction of SST dependence and year contributed less for gill net surveys (Table 4). The annual partial response curve showed a monotonous increase with SST above 10°C within the observed range ( $6.1-17.1^{\circ}$ C) in most years (an example from 1987 in Fig. 6c,d).

Table 3. Approximate significance and change in Akaike's information criterion ( $\Delta$ AIC) of each explanatory variable of the best model for the weight of sardine catch per fishing operation (catch per unit effort, CPUE, in tonnes) by purse seine fisheries (deviance explained = 69.5%). Summary of the smooth terms for (lon, lat)<sub>year</sub> and SST<sub>year</sub> is provided in Table S3 in the Supplement. The top 5 models are provided in Table S4. Abbreviations are defined in Table 2

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Smooth terms	edf	Ref.df	F	р	ΔΑΙΟ
year (lon, lat) (lon, lat) <sub>year</sub> SST SST <sub>year</sub>	9.00 24.60 4.15	9.00 27.22 5.15	54.74 21.38 9.71	<0.001 <0.001 <0.001	251 106 640 23 301

Table 4. Approximate significance and change in Akaike's information criterion ( $\Delta$ AIC) of each explanatory variable of the best model for the number of sardines caught per net (catch per unit effort, CPUE) by the gill net surveys (deviance explained = 52.3%). Summary of the smooth terms for (lon, lat)<sub>year</sub> and SST<sub>year</sub> is provided in Table S5 in the Supplement. The top 5 models are provided in Table S6. Abbreviations are defined in Table 2

Smooth terms	edf	Ref.df	F	р	ΔAIC
year (lon, lat) (lon, lat) <sub>year</sub> SST SST <sub>year</sub>	7.86 22.86 3.44	8.39 26.38 4.27	14.40 4.10 5.57	<0.001 <0.001 <0.001	80 40 185 8 15



Fig. 5. Partial response curves showing the effect of year on the catch per unit effort (CPUE) for (a) large- and mediumtype purse seine fisheries and (b) the gill net surveys. The y-axis represents the standardized partial regression coefficient. Dashed curves indicate 95 % confidence intervals

# Model predictions: CPUE

The mean predicted CPUE showed similar year trends to the observed value for both fishing methods (Fig. S2 in the Supplement). However, the extrapolation failed to predict realistic CPUE on the grid where observations were not available, because of limited data. Therefore, predicted values that were larger than the maximum observed value were removed from the calculations of mean and SD. The decadal mean and SD of predicted CPUE per grid point at a 0.5° longitude and latitude interval demonstrated that CPUE of purse seine fisheries was high around the Oki Islands and changed slightly in space during the 1980s and 1990s (Fig. 7a,b). CPUE of gill net surveys was high in the northern offshore area of the Sea of Japan in the 1980s (Fig. 7c-2). The best model failed to predict CPUE from 1990 to 1992, resulting in high values over a wide area (Fig. 7c-3).

# Distribution area and stock biomass

The distribution area, given by the fraction of the grid points with a presence probability greater than 0.46, increased rapidly after 1975, peaked in the



Fig. 6. Partial response curves showing the effect of sea surface temperature (SST) on the catch per unit effort (CPUE) in 1987 for (a) large- and medium-type purse seine fisheries and (c) gill net surveys. The y-axis represents the standardized partial regression coefficient. Dashed curves indicate 95% confidence intervals. Annual changes in the effect of SST on (b) large- and medium-type purse seine fisheries and (d) gill net surveys. Dashed line with filled circles indicates the range of SST with positive standardized partial regression coefficient



Fig. 7. (a,c) Mean and (b,d) standard deviation maps of predicted catch per unit effort (CPUE) per decade per grid point at a 0.5° longitude and latitude interval. (a) and (b) are for large- and medium-type purse seine fisheries, (c) and (d) are for gill net surveys. Note that gill net surveys for the 1970s were conducted from 1975 to 1979, and those for the 1990s were conducted from 1990 to 1992

early 1980s, and then gradually decreased in the decades after 1983 (Fig. 8). The biomass of Japanese sardine started to increase from 1970, peaked in 1989, but noticeably declined in the decade immediately after 1989 (Ohshimo et al. 2009). The cross-correlation analysis indicated that the correlation coefficient was highest (0.76) at the lag -1 years for the trajectory of the distribution area and that of stock biomass (Fig. S3 in the Supplement). In addition, a 3 yr moving average of distribution area reached a maximum in 1982, but that of stock biomass reached a maximum in 1987. There was a time lag between the peaks of distribution and biomass.

# DISCUSSION

Our analyses showed that the distribution of the Japanese sardine subpopulation in the Sea of Japan during spring (from March to May) started to expand from the late 1970s and peaked in the early 1980s, before stock biomass peaked (Fig. 8). The distribution then gradually contracted in the decade after 1983. A GAM that simultaneously handled 2 different sources of data demonstrated the noticeable expansion in the distribution of Japanese sardine in the northern area. Sardines were caught by gill net surveys in the northern offshore area, but south of the polar front



Fig. 8. Fraction of the grid points with a presence probability greater than 0.46, illustrated by a bold line with a filled circle. Dashed lines indicate 95% confidence intervals. Open circles indicate the stock biomass per Ohshimo et al. (2009)

(Fig. 4c). In contrast, the area where sardines were caught by purse seine fisheries was consistently along the coastal area of Honshu Island and Kyushu Island, and only slightly expanded to the south and offshore during the 1980s (Fig. 4a). The CPUE of the gill net surveys peaked in the early 1980s (Fig. 5b), when sardines were caught at most of the survey points (Fig. 2b). In contrast, the CPUE of the purse seine fishery was higher from 1985 to the early 1990s (Fig. 5a), when stock biomass was high (Fig. 8).

Geographical changes in distribution area have been reported for different sardine populations. Sardine and anchovy populations off the coasts of California, Peru, South Africa, and Japan (northwest Pacific Ocean) simultaneously expanded and shrunk with increases and decreases in stock biomass. These changes were reflected in their packing density, and were attributed to population growth and decline (Barange et al. 2009). The changes in distribution, accompanied by fluctuations in population abundance, were considered the result of density-dependent habitat selection (DDHS), under the assumption that each individual follows the ideal free distribution and receives the same amount of resources (Fretwell & Lucas 1969, MacCall 1990). If the transmigration of individuals requires time, the expansion in distribution may be delayed after biomass explosion, while the contraction of the distribution area may occur after biomass collapse. In this case, distribution may be altered following changes in biomass. However, our results showed that the distribution area

began expanding during the initial phase of population expansion, and started contracting before the stock biomass trajectory peaked. Thus, DDHS does not represent the mechanism for the changes in the distribution of the sardine population inhabiting the Sea of Japan.

A density-independent process has the potential to determine the geographic distribution of small pelagic fish. For example, environmental conditions influence the habitat selection and migration of fish (Fréon & Misund 1999). SST represents an important determinant of habitat for sardines and anchovy (Rodriguez-Sanchez et al. 2002, Emmett et al. 2005, McFarlane et al. 2005). In addition, salinity and chlorophyll *a* concentrations are associated with the catch rates of Pacific sardines (Emmett et al. 2005). On the basis of our results, we considered how changes to SST in the Sea of Japan from the 1970s to the 1990s may have influenced the

spatio-temporal dynamics of the sardine population. In addition, we discuss 2 mechanisms, i.e. primary production and ocean currents, that possibly induce changes in spatio-temporal dynamics.

# Sea-surface temperature

We examined whether SST-dependent habitat selection produced the observed change in sardine distribution. Oceanographic conditions in the Sea of Japan and East China Sea noticeably changed with a climate regime shift during 1976–1977 and 1988– 1989 (Hare & Mantua 2000). A strong Aleutian low pressure system intensified winter wind stress over northern Japan, resulting in winter SST decreasing, especially in the coastal area to the north of the polar front (approximately 38° N; Isoda 1994). The mean SST of the whole Sea of Japan during March and May was generally low from 1977 to 1988 and from 1997 to 1999, but was high from 1989 to 1996 (Fig. S4 in the Supplement).

The interaction of SST dependence and year were included in the best models for both presence/ absence and CPUE. Sardines were caught in SSTs ranging between 5 and 23.8°C (observed maximum SST; Fig. 3) and CPUE showed positive SST dependence over 6.5°C (Fig. 6). An experimental study reported the preferred SST of sardine to be 20°C, while the critical thermal minimum was 3.5°C (Tsuchida 1995). The growth rate had a dome-shaped relationship with SST from 11.8 to 20.2°C, peaking at 16.2°C (Takasuka et al. 2007). These results indicate that Japanese sardine are able to inhabit a wide range of temperatures, despite indications of a preferred temperature. A similar SST range was reported for the presence of Pacific sardines (7–28°C; Parrish et al. 1989). In addition, the flat-topped shape of the probability curve over a wide range of SSTs masked the importance of annual variation (Figs. 3b & 6b,d). Thus, it was difficult to determine whether SST-dependent habitat selection caused the expansion and contraction in the distribution of the sardine sub-population in the Sea of Japan.

## Primary production: bottom-up mechanism

A change in primary production may induce changes to individual survivorship and/or the migration process, resulting in the changes to the distribution. A slight decrease in chlorophyll a (chl a) concentration and a noticeable decrease in zooplankton wet weight were observed in the spring after 1976 in the southern Sea of Japan (south of ~38°N) and Korean waters (Zhang et al. 2000, Chiba et al. 2005). In contrast, both chl a concentration and zooplankton net weight slightly increased in the northern offshore region of the Sea of Japan (Chiba et al. 2005). Chl a concentration was positively correlated with primary production in the offshore area of the Sea of Japan (Nagata 1998), and also with sardine presence in other areas (Garrido et al. 2008, Lanz et al. 2009, Zwolinski et al. 2010). Theoretically, sardine may have preferred the northern and offshore areas of the Sea of Japan where the feeding environment was better, compared to that in the south. Alternatively, sardine may have been transported to the north, resulting in better offshore survival, due to the enhanced feeding environment. However, chl a concentration remained relatively high in the northern Sea of Japan during the early 1990s, when the distribution area started to contract (Chiba et al. 2005). The bottom-up mechanism might explain the expansion in sardine distribution, but does not seem to explain habitat contraction.

# Ocean currents and spawning grounds: transport-system-change mechanism

A change in transport system may have caused the expansion in sardine distribution. The TWC has 3 branches: the first flows along Honshu Island, the

second flows offshore with large meanders, and the third flows northward along the east coast of Korea (Senjyu 1999; Fig. 1). In association with the shift in the climate-ocean regime, inflow of the TWC from the Tsushima/Korea Strait to the Sea of Japan increased from 1976 to the late 1980s (Isoda 1994). In parallel, the major spawning ground of Japanese sardine moved southwards, and spread along the northern coast of Kyushu Island, during the cold-water period (Goto 1998). Thus, the third branch of the TWC may have transported larvae and juveniles that spawned in the north of Kyushu Island northwards and offshore in the Sea of Japan. During the 1990s, the inflow of the TWC decreased (Isoda 1994), and the major spawning ground moved northwards, spreading along the middle part of the coast of Honshu Island (Goto 1998). Under this scenario, the first branch of the TWC may have caused most of the larvae and juveniles to be retained around Honshu Island, with less transportation northwards, resulting in the contracted northern distribution area.

Thus, the transport-system-change mechanism may provide an underlying mechanism for changes in sardine distribution, because most of the sites where sardines were caught were located below the polar front and in the flow of the TWC (Fig. 4). In addition, the bottom-up mechanism may explain why sardine distribution expanded, because it improved the survivorship of individuals transported northwards and offshore. Unfortunately, we did not have enough data to examine these mechanisms. Further investigations on the dispersal process of Japanese sardine in the Sea of Japan and East China Sea, such as surveys on the distribution of the early life stages and particle-tracking studies, are required.

The time lag in year trends of CPUE between the 2 fishing methods was consistent with the result of the presence/absence model (Figs. 2 & 5). This result suggests that the catch (CPUE), as well as the potential distribution, changed during the shift in the climate-ocean regime. However, further information about fishing characteristics may be necessary for standardizing CPUE. For example, gill net surveys were conducted at night by drifting a series of mesh panels. Purse seine fisheries generally operated at night using an echo sounder to search for schools of fish and a fishing light to harvest them, yet they operated without echo sounders during the 1980s when Japanese sardine were widely and densely distributed (S. Ohshimo pers. obs.). Searching methods for targeting aggregations could maintain catch rates under circumstances of declining stock level, resulting in hyperstability of the relationship between

stock abundance and CPUE (Hilborn & Walters 1992). In addition, fishermen would change target species according to resource condition. Such fishing characteristics would cause some biases for calculating long-term changes in CPUE, but could not be incorporated in the present analysis due to lack of detailed information. Therefore, our catch data could examine the cause-and-effect relationship not between the potential distribution area and non-zero catch and stock biomass. Future studies on the mechanisms that drive changes in habitat distribution and its relationship with fluctuating fish stock biomass might reveal the underlying drivers of sardine population dynamics, and contribute to improved management of these stocks.

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